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HISTORICAL EVIDENCE AS TO THE ORIGIN OF THE PAIRED LIMBS OF VERTEBRATES.

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WHATEVER be the results of embryologists, the real test of the problem of the mode of origin of the paired limbs of vertebrates belongs obviously to paleontology. For if the paired limbs, as most morphologists believe, arose as highly specialized lappets of a continuous lateral skin fold, it is quite evident that sooner or later these conditions will be demonstrated convincingly among the earlier fossil fishes. In point of fact, the paleontological evidence bearing upon this matter is of such great value, even at the present time, that we can justly regret that it has received scanty attention at the hands of embryologists. It is indeed so imperfectly noticed in the recent voluminous papers which bear upon the general problem of limb origin that I have been led to the following comments.

I. THE WEIGHT OF EVIDENCE.

If we accept the general rule that earlier forms are of greater value for purposes of determining primitive characters than are later ones, and if we admit that a study of many genera and many species is of greater value than an examination of few specimens of few species, we must, I believe, conclude that the doctrine of the origin of the paired limbs from lateral dermal folds rests upon strong foundations. Reducing to simplest terms our knowledge of the earliest sharks or shark-like fishes, among which the ancestral jaw-bearing vertebrates are reasonably sought, we find that of forty odd species, representing fifteen genera (Paleozoic), whose fin characters are known, all but those of a single genus, and possibly a second, are distinctly in favor of the lateral-fold theory. And the exceptions to the rule are the most recent forms and in important structural regards the least primitive.

More concretely, such genera as the Upper Silurian and Lower Devonian Parexus (two species), Climatius (eight species), Diplacanthus (five species) (= family Diplacanthidæ), Cheiracanthus (three species) (Acanthodidæ), and the long-enduring Acanthodes (twelve species) (Lower Devonian to Permian); as the Upper Carboniferous Acanthodopsis (but we may put the last aside, since its fin structures are not as well known as in the neighboring forms); as the Permian Protacanthodes and Traquairia, — all of these ancient sharks have their paired limbs in the form of distinct longitudinal skin folds, and these paired fins, furthermore, are essentially similar to the unpaired ones. This conclusion is based upon numerous and well-preserved specimens. The next ancient sharks whose fin structures are described are the (now accepted as) Upper Devonian cladoselachids (about two genera and six species). These have the paired fins extended along the body, their hinder web narrowing gradually and merging with the body wall, showing no trace of a lobate fin base projecting from the body. Here, too, the paired fins closely resemble the unpaired fins. Structural details in these forms are known from a score or more of well-preserved specimens. A kindred Upper Devonian shark is Ctenacanthus, whose fin structures have hitherto been unknown; but an interesting specimen of this form, showing pectoral fins and spine *in situ*, has now been discovered, and it shows convincingly that this shark had a fin-fold type of fin. Its radials pass to the margin of the fin, as in Cladoselache, each with a corresponding basal; unlike cladoselachids, there are no intercalated rays. Next ancient is Traquair's specimen of Cladodus (Lower Carboniferous) (*cf.* Fig. 1), whose pectoral gives evidence of a line of basal plates extending backward like

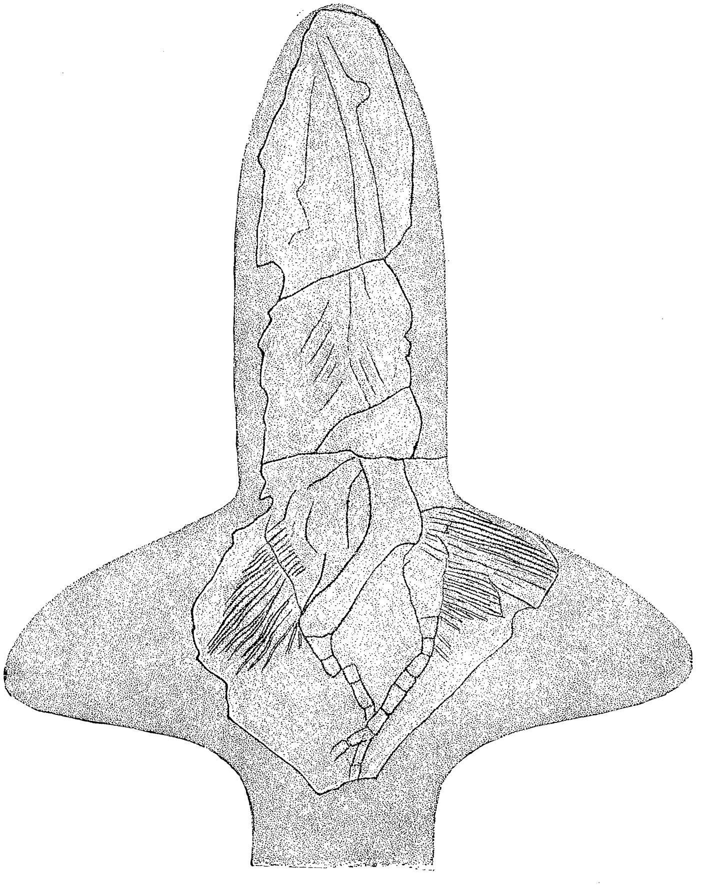

FIG. 1. — The Paleozoic shark *Cladodus neilsoni* Traquair. The fossil is shown surrounded by the outline of a specimen of Cladoselache of similar size, — indicating that the fins of Cladodus were of larger size than the present fossil suggests.

a rayless axis of an "archipterygial" fin. This specimen has been taken in evidence of the non-primitive nature of the fin-fold type of limb (*vide infra*). Last of the ancient forms are the Permian symmoriids and xenacanthids. Of these Symmorium, judging from the single fragmentary pectoral described by Cope, is similar to cladoselachids, but remarkable in that its hindmost rays apparently coalesce at their bases so as to form a stout supporting plate. There is no evidence, however, that this projected from the body wall, nor have we any knowledge of pelvic or unpaired fins. In xenacanthids, on the other hand, many and well-preserved specimens (of two or three species) show a biserial archipterygium in the pectoral fin, and this condition has been the main paleontological stay of those who oppose the fin-fold hypothesis. They lay no emphasis, however, on the late appearance of this form (for there is no evidence forthcoming that the Coal Measure "Xenacanthus" had fins like the Permian form), or on the facts that its ventral fin is *not* a biserial archipterygium but resembles closely the unpaired fins immediately behind it, and that this form has already developed a mixipterygium, and has specialized an amphistylic attachment of jaw to skull, and that it has largely lost its integumental defenses.

Balancing the matter fairly, I think that we must conclude that the weight of the evidence of Paleozoic sharks falls emphatically on the side of the longitudinal fin-fold hypothesis. Indeed the only way, as far as I can see, in which this evidence can be denied is by a frank rejection of the well-accepted view as to the primitive nature of the earliest elasmobranchs (Proselachii).

II. THE FIN-FOLD CHARACTER OF THE EARLIEST FORMS, ACANTHODIANS AND CLADOSELACHIDS.

The dermal-fold nature of the paired fins of the acanthodians requires little comment. Excepting in a brief note of Dr. Fritsch,[1] no attempt has ever been made to explain them in accordance with the theory of Gegenbaur; that is, that their origin is due to outgrowth of elements belonging to serially homologous gill bars. Continuous fin folds they certainly are, whether or not we accept the origin of their supporting elements as equivalent to the coalesced radial supports of a more typical shark-like fin. On the other hand, the paired fins of the cladoselachids are distinctly shark-like, although in pattern unlike those of later selachians. They are remarkable in that they are built on the plan of balancing organs; *i.e.*, the fin was attached keel-fashion, along the side of the body, and probably functioned by means of ventrad and dorsad movements (undulatory at fin margin ?). And the blade of the fin could not be rotated (twisted) sideways. This is attested structurally by (1) its graded series of radials, — larger, most numerous, and most crowded in the anterior region; (2) by the absence of a metapterygial lobe, and in the continuation of the fin web hindward along the margin of the body; physiologically (3) by its close analogy with the dorsal and anal of such a form as Mola, in which we know that this undulatory movement has been specialized. That the paired fins of Cladoselache, moreover, cannot be interpreted as "due to bottom living" on the plan, *e.g.*, of Rhina, becomes clear when we consider that the radial cartilages are unjointed throughout their length, that the ventral and pectoral fins are not drawn together in a ray-like way, and that the fins, in spite of their remarkable character, are *as small in proportion to the size of the body as those of modern selachians* (Pristiurus, Scyllium), *which are known to be free swimming*. (*Cf. Natural Science*, Vol. VIII (1896), pp. 250–252, and *Anat. Anzeiger*, Bd. XI, pp. 673–679. *Vide* also *infra*.)

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[1] *Fauna d. Gaskohle Formations Böhmens* (1893, p. 71), in which the spine is regarded as the archipterygium. Dr. Jaekel homologizes shoulder girdle to gill arch, but does not consider the relations of the fins themselves. *Verhandl. Deutschen Zool. Gesell.* (1899), pp. 256–258.

III. The Evidence of Paleontology as to the Development of the Unpaired Fins.

In recent work tending to support the hypothesis of Gegenbaur no reference is made to the mode of origin of the unpaired fins. This, we must grant, would have an important bearing upon the problem of the extremities if evidence existed to show that in a late stage in the evolution of the unpaired fins an archipterygium arose, like that of the paired fins. As a matter of fact, paleontology demonstrates that such a condition is represented in the case of the ancient ganoids (crossopterygians); for in certain Devonian forms (*cf.* also Mesozoic genera) the dorsal fins show clearly concrescence of radial and basal elements in a way which parallels strikingly the biserial archipterygium (of the paired fins).[1] This condition, although well known to the paleontologist, appears to have escaped the notice of the adherents to the Gegenbaurian school. It is perfectly evident that if the biserial archipterygium arises in the unpaired fin from the concrescence of lateral fold-like supporting elements, the similar structure in the paired fins must have arisen in a similar way, or, to say the least, the burden of disproof lies with those who believe that such closely similar structures arose by diametrically opposite processes.

IV. CONCLUSION.

The evidence of Paleozoic sharks, then, is most distinctly in favor of the Thacher-Balfour teachings. The oldest forms, acanthodians and cladoselachids, represented by the best-preserved fossils present lateral-fold fins. Moreover, there is evidence that as the series advances from the Lower Devonian, the structures of the biserial archipterygium are gradually acquired. The Carboniferous *Cladodus neilsoni*, Fig. 1, of Traquair shows for the first time a definite segmentation of the supporting elements of the base of the pectoral fin.[2] Then in the Permian Symmorium Cope, the fin bases not only are formed, but show apparent fusion in the metapterygial region, and even perhaps an extension from the body wall of the metapterygial terminal, a condition which would be best correlated with a change of function in the fin. And finally, in the xenacanthids, whose structures are known only in this later horizon, the pectoral fin acquires a biserial archipterygium. The conditions, however, of *Cladodus neilsoni* and of Symmorium are still doubtful, the present knowledge of them having been based upon single, imperfectly preserved, and fragmentary specimens. The conditions in Cladoselache, on the other hand, are known from upward of thirty specimens, some of which are admirably preserved.[1] In conclusion, if the Gegenbaurian adherents are to contest the sum and substance of the paleontological evidence, they have, it seems to me, the difficult task of demonstrating (1) that acanthodians, the most extensive group of Paleozoic sharks, do not possess pleuropterygia; (2) that Cladoselache, in spite of its earlier occurrence and peculiar structures, is not as archaic a type of shark as Xenacanthus; and (3) that the "archipterygium" formed in the unpaired fins as the terminal member of a series whose original structures were of fin-fold character, is formed in exactly the opposite way from the archipterygium in the paired fin. Until these contradictions have been disposed of, no evidence based upon recent forms can, I believe, attack the main trenches of the lateral-fold theory.

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[1] *Cf.* also the anals of Xenacanthus.

[2] Judging from the size of the shark and the character of the radials, the pectoral fin was probably larger, and there is thus ground to believe that the posterior radials of the fin have been lost. This is better understood by reference to the accompanying Fig. 1, where the Scottish specimen is shown overlaid with an outline of Cladoselache of similar size.

Postscriptum. — *Objections which have been urged to the foregoing conclusions.*

As far as I am aware, no objections have been raised to the conclusion that the paired fins of the acanthodians represent definite lateral dermal folds, whatever may be regarded as the homologues of the supporting elements of these fins. (Thus Fritsch endeavors to find in the pulp canals of the anterior fin spines rudiments of an entire biserial archipterygium (*Fauna d. Gaskohle Formations Böhmens*, Bd. III, p. 71). (As a corollary to this suggestion, I take it, the fin spines of *all* acanthodian fins are equivalent to archipterygia, since the spines are similar in structure in all fins!) Cladoselache, however, has been subjected to adverse criticism by several advocates of Gegenbaur's hypothesis. Professor Jaekel, the first of these critics, is the only one who appears to have had the opportunity of examining actual specimens of this form, for during his visit to

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[1] Sections of the muscle plates have been found to show transverse striæ in the fossilized muscle cells. Their description will shortly be published.

New York he inspected some of the material obtained by Professor Newberry for the museum of Columbia University. He regarded "Cladodus" as a shark which had become highly specialized and adapted to bottom living. Against this view it is merely necessary to note that Cladoselache possessed dorsal fins, one of which was situated well forward on the trunk region, its anterior rim lying above the pectoral fin, a condition entirely unknown in any depressed type; that the caudal fin was of a peculiar form, extreme in its heterocercy, and provided on either side with broad, stout lateral flanges closely comparable to those of such swift-swimming forms as Isurus, or even scombroid fishes. It is evident that none of these characters can be associated with a bottom-living form such, for example, as Rhina. Moreover, *if Cladoselache were a bottom-living form, its fins would obviously have been larger in proportion to the size of the animal than those of recent sharks.* In this connection, however, it is only just to Dr. Jaekel to state that at the time of his visit to Columbia University none of the best material of this form had yet been obtained, — that the caudal and dorsal fins, for example, were not known.

A second writer, Professor Semon, in one of his studies on Ceratodus (*Forschungsreisen,* Bd. I (1898), pp. 105–106), subscribes to a page of general denial as to the primitive nature of Cladoselache. As he does not, however, refer to the detailed literature upon this form, quoting only from a single and semi-popular article, and in view of other omissions, I am inclined to believe that his criticism is inadequate. Thus I note that he is unaware that the horizon of Cladoselache is now conceded (*cf.* Orton and others) to be Upper Devonian instead of Lower Carboniferous, and that he puts this form in the Coal Measures side by side with xenacanthids, whose structural characters are known only from the Permian; also that he states that *dipnoans* (he does not mean by "dipnoans," I take it, the very problematical arthrodires, since these are naturally included in the term "placoderm," which he specifically mentions) *and crossopterygians were already present in Silurian times,*—a statement I can only account for on the basis either that he has collected data which, when published, will throw light upon this empty page of the geological record, or that by Silurian he means Devonian, an age in which, by the way, we must admit that Cladoselache occurs. He surely cannot refer in the above terms to the minute fragments of Ostracophores of Oesel, which were once, about a decade ago, referred to as ganoidean and dipnoan.

And most recently Dr. Braus[1] has considered in a special paper the later discoveries in fin structures in fossil selachians, and has even concluded that "through paleontology the theory of Gegenbaur has been given new life." Braus, however, makes no reference in this connection to the archipterygial characters of unpaired fins, nor yet to acanthodians, and furthermore, he treats all extinct forms without reference to their different geological horizons. The pectoral fin of Cladoselache he regards as essentially similar to that of Chlamydoselachus, believing that its metapterygial region has been obscured by the overlying body wall during the process of fossilization, and that the fin in reality possessed a lobate base which projected from the body wall, as in the recent shark. He accordingly must believe that the continuous posterior dermal margin of the fin in the fossils, as several writers have figured it,[2] is not a just one. I think, however, that I am justified in stating that this reactionary view finds no support in any known[3] specimen of this form. And I may further add that the line which continues the web of the lappet-shaped fin along the side of the body, which Braus is skeptical about, and which is hostile to the Gegenbaurian theory, is preserved in faultless condition in as many as a dozen specimens which are now under my hands. Braus further believes that the ventral fin of Cladoselache shows a trace of a distinct metapterygium (as of Chlamydoselachus), inasmuch as radials occur in the hinder portion of the fin web, a conclusion to which I do not understand the *sequitur*. The absence of mixipterygium in cladoselachids (as well as in acanthodians, in fact the whole matter of the acanthodians) he does not consider in this connection.

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[1] *Verhandlungen d. Phys.-Med. Gesellsch. zu Würzburg* (N.F.), Bd. xxxiv (1901), pp. 177–192; *cf.* also *Zool. Forschungsreisen*, Bd. i (1901), Lieferung III, pp. 197, 266, 268.

[2] The fin margin has thus been figured — rounding in along the body wall — undissentingly by at least four authors. Braus does not consider this important feature of the fin, which I am sure he would have felt bound to do had he examined actual specimens.

[3] I speak confidently, since I have good reason to believe that all cladoselachids have hitherto been obtained through three collectors in Ohio, whose output I have had the opportunity of examining.

Braus, in summary, teaches that paleontological discoveries lead to the "overwhelming conclusion" that the recent shark fin has acquired its typical form of skeleton through a process of reduction wherein the original terminal and post-terminal axial portions have become lost, while the pre-axial region has developed and with it its basal plates. The reviewer, however, must confess that he finds it rather difficult to determine exactly how Braus has obtained these paleontological results, unless by deriving the Devonian forms from the Permian ones, — which, in view of the many remarkable structural characters of Cladoselache (which Braus also, by the way, does not consider), appears as unconvincing as a process which derives the Miocene Protohippus from the Pliocene horse.